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CLIMATE CHANGE INDUCED VEGETATION SHIFTS IN THE PALEARCTIC REGION

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Abstract. Global average temperature has increased and precipitation pattern has altered over the past 100 years due to increases in greenhouse gases. These changes will alter numerous site factors and biochemical processes of vegetative communities such as nutrient and water availability, permafrost thawing, fire regime, biotic interactions and invasion. As a consequence, climate change is expected to alter distribution ranges of many species and communities as well as boundaries of biomes. Shifting of species and vegetation zones northwards and upwards in elevation has already been observed. Besides, several experiments have been conducted and simulations have been run all over the world in order to predict possible range shifts and ecological risks. In this paper, we review literature available in Web of Science on Europe and boreal Eurasia and give an overview of observed and predicted changes in vegetation in these regions. The main trends include advance of the tree line, reduction of the alpine vegetation belt, drought risk, forest diebacks, a shift from coniferous forests to deciduous forests and invasion. It is still controversial if species migration will be able to keep pace with climate change.
Keywords: *global warming, vegetation distribution, biome, vegetation zone, plant community*

Introduction

Increases in greenhouse gases, especially in carbon dioxide, are expected to increase average surface temperatures and alter precipitation patterns (Ryan, 1991). Over the past 100 years, the global average temperature has increased by approximately 0.6 °C and is expected to increase by 1.4 to 5.8 °C in the 21st century (IPCC, 2001). These changes will alter numerous biochemical processes of vegetative communities (Drégelyi-Kiss et al., 2008). Changes in growth rates, carbon allocation patterns, nutrient cycling and competitive interactions will lead to changes in the structure and species composition of many plant communities (Ryan, 1991; Grime et al., 2008). As a consequence, climate warming is expected to alter distribution ranges and boundaries of many species (Van der Veken, 2004), and both latitudinal and altitudinal shifts in vegetation zones will occur in many regions, across a wide range of taxonomic groups (Ryan, 1991; Walther, 2004; Peñuelas et al., 2007; Bertrand et al., 2011).

Distribution changes caused by climate change are partly related to species-specific physiological thresholds of temperature and precipitation tolerance (Woodward, 1987). However, the possible impact of climate change on plant distributions depends on several natural and anthropogenic factors, such as the rate of climatic change, landscape

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fragmentation, seed availability, resource availability, dispersal capabilities of individual species and interactions with land use (Walther et al., 2002; Thuiller et al., 2005; Engler & Guisan, 2009; Buetof et al., 2012) as well as on grazing e.g. by wild ungulates (e.g. Kullman, 2001; Grace et al., 2002; Moen et al., 2004). Besides, successful poleward shifts of plant species ranges will depend on interactions between migrating species and the communities they invade (Moser et al., 2011). In Arctic terrestrial ecosystems, geographical barriers such as the distribution of landmasses and separation by seas, will affect the northwards shift in vegetation zones (Callaghan et al., 2004).

Climate change will alter, beside temperature and precipitation, other site factors as well, in the first instance the water balance at the site (Wattendorf et al., 2010). Climate, vegetation and fire are interrelated so that any change in one will affect the others. Climate-driven changes in the structure and composition of plant communities will affect fire potential by altering the physical and chemical properties of fuels and vice versa, changes in timing and severity of fire will modify the rate at which communities respond to climate change (Ryan, 1991).

Vittoz et al. (2009) conclude that vegetation communities can respond rapidly to warming as long as colonization is facilitated by available space or structural change. Climate disturbances, such as exceptional drought, may accelerate community changes by opening gaps for new species. Walther (2010) assumes that biotic interactions and feedback processes can lead to highly complex, nonlinear and sometimes abrupt responses. According to Meier et al. (2012), it remains unclear if species will be able to keep pace with recent and future climate change. They conclude that migration rates depend on species traits, competition, spatial habitat configuration and climatic conditions, and re-adjustments of species ranges to climate and land-use change are complex and very individualistic. Inter-specific competition, which is higher under favourable growing conditions, reduces range shift velocity more than adverse macroclimatic conditions do, and habitat fragmentation can also lead to considerable time lags in range shifts. According to their simulations, Meier et al. (2012) found that early-successional species track climate change almost instantaneous while mid-to-late-successional species migrate very slowly. Distributions of early-successional species during the 21st century are predicted to match quite well with the unlimited migration assumption (i.e. mean migration rate over Europe for A1Fi/GRAS climate and land-use change scenario is 156.7 +/- 79.1 m/year and for B1/SEDG 164.3 +/- 84.2 m/year). Predicted distributions of mid-to-late-successional species match better with the no migration assumption (for A1fi/GRAS: 15.2 +/- 24.5 m/year and for B1/SEDG: 16.0 +/- 25.6 m/year).

Skov and Svenning (2004) studied the impacts of climate change on forest herbs in Europe and predict that the total suitable area of the studied species will move strongly northwards and moderately eastwards under the relatively mild B1 scenario and more strongly so under the A2 scenario. The required average minimum migration rate per year to track the potential range shift is 2.1 km under the B1 scenario and 3.9 km under the A2 scenario, which is incomparably larger than the migration rate predicted by Meier et al. (2012). Thus, for most species, moderate losses in the total suitable area are predicted under both scenarios. However, expected changes are very variable for the individual species, from total range elimination to large increases in total suitable area.

Neilson et al. (2005) assume that the rate of future climate change is likely to exceed the migration rates of most plant species. The replacement of dominant species by

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locally rare species may require decades, and extinctions may occur when plant species cannot migrate fast enough to escape the consequences of climate change. According to Neilson et al. (2005), migration processes cannot be confidently simulated in dynamic global vegetation models. Schwartz (1992) also assumes that shifts in composition within plant communities are likely, but are, as yet, unpredictable. Migration capabilities of species are questioned by Malcolm et al. (2002) as well. According to their simulations, high migration rates (greater than or equal to 1000 m/year) will be relatively common, however, they will be much higher in boreal and temperate biomes than in tropical ones. Malcolm et al. (2002) conclude that global warming may require migration rates much faster than those observed during post-glacial times and hence has the potential to reduce biodiversity by selecting for highly mobile and opportunistic species.

Lags between biotic responses and contemporary climate changes have been reported for plants and animals by Bertrand et al. (2011). Theoretically, the magnitude of these lags should be the greatest in lowland areas, where the velocity of climate change is expected to be much greater than that in highland areas (Bertrand et al., 2011). According to the study of Bertrand et al. (2011), forest plant communities had responded to 0.54 °C of the effective increase of 1.07 °C in highland areas (500-2,600 m a.s.l.) between 1965-2008 in France, while they had responded to only 0.02 °C of the 1.11 °C warming trend in lowland areas. Thus, there was a much larger temperature lag between climate and plant community composition in lowland forests than in highland forests. Such disparity can be caused by the higher proportion of species with greater ability for local persistence as the climate warms, the reduced opportunity for short-distance escapes, and the greater habitat fragmentation in lowland forests. Schwartz (1992) also assumes that migration response is likely to lag far behind rates of climatic change, potentially threatening narrowly distributed species whose predicted future ranges do not overlap with their current range. According to Schwartz (1992), predictions of species' northward range shifts in response to climate change vary from 100 km to over 500 km. In the past, tree species typically migrated at rates of 10 km to 40 km per century.

Effects of climatic warming and elevated CO_2 on plants are likely to be different for different species (Werkman & Callaghan, 2002; Baselga & Araujo, 2009). The response of one species within a functional type cannot predict the response of another (Klanderud, 2008). Neither can plant species with similar climatic niche characteristics be expected to respond consistently over different regions, owing to complex interactions of climate change with land use practices (Buetof et al., 2012). Thus, geographical variability can be observed in responses of species and ecosystems to environmental change (Callaghan et al., 2004).

As far as dispersal and resource availability allow, species are expected to track the changing climate and shift their distributions poleward in latitude and upward in elevation (Aaerts et al., 2006; Davis & Shaw, 2001; Theurillat & Guisan, 2001; Walther et al., 2002). It is also expected that some previously unforested regions at high latitudes and altitudes (i.e. the cold treeline) may become more suitable for tree growth, while some low-latitude and low-altitude areas may not sustain forests any more due to an increase in droughts (Cairns et al., 2007; Gehrig-Fasel et al., 2007). There is already evidence that such changes in species ranges have occurred during the 20th century, e.g. the tree line has advanced towards higher altitudes in Europe (Meshinev et al., 2000; Kullman 2001), and alpine plants have shown elevational shifts of 1-4 m per decade

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(Grabherr et al., 1994). The “up-greening” of northern tundra sites (Myneni et al., 1997) and the upward shift of larch populations in the Alps (Martinelli, 2004) were observed as well. Another evidence for an upward movement of species along elevational gradients is the increase in species richness on mountain tops and an increase of the floristic similarity of the summits (Walther et al., 2005; Jurasinski & Kreyling, 2007). However, the development on single summits is not strictly unidirectional, there may also be species with opposing trends, i.e. remaining in place or even moving downwards (Jurasinski & Kreyling, 2007; Frei et al., 2010). Thus, there is a dynamic balance between upward advances (colonisation), encouraged by favourable environmental conditions, and retreats (extinctions), caused by adverse conditions (White, 1996). Species from lower elevations or latitudes may invade faster than resident species are receding upward or poleward, which results in a (probably transient) increase in species diversity of the considered community (Aaerts et al., 2006).

In this paper, observed and simulated changes of community composition and range shifts are reviewed all over Europe, based on literature available in Web of Science. In this case, the focus is on different parts of Europe in a geographical sense and not on vegetation types. As a first step, we review modelled vegetation changes related to the whole world and continue with discussing changes in Europe.

Climate change induced vegetation shifts all over the world

Some authors studied the effects of climate change on vegetation related to the whole world and predicted the shifts of different vegetation zones. However, their approaches are quite different that is why their results do not always coincide with each other.

Climate change threatens to shift vegetation and disrupt ecosystems (Gonzalez et al., 2010). Field observations in boreal, temperate and tropical ecosystems have detected biome changes in the 20th century. According to the study of Gonzalez et al. (2010), one-tenth to one-half of global land may be highly to very highly vulnerable to climate change. Temperate mixed forest, boreal conifer forest, tundra and alpine biomes show the highest vulnerability, often due to potential changes in wildfire, while tropical evergreen broadleaf forest and desert biomes are predicted to be the least vulnerable. According to Thuiller et al. (2008), although increasing evidence shows that recent environmental changes have already triggered species' range shifts, accurate projections of species' responses to future environmental changes are difficult to ascertain.

Köhler et al. (2005) presume the collapse of the North Atlantic thermohaline circulation. In this case, the cooling of the northern hemisphere is predicted. As a consequence, a dieback of trees is expected in high latitudes, a reduction in the extent of boreal and temperate forests and a southward movement of the tree line. Precipitation changes are predicted to cause a persistent replacement of grass by raingreen trees in a few subtropical areas.

However, other authors do not consider the potential collapse of the North Atlantic thermohaline circulation that is why they come to other consequences. Claussen and Esch (1994) predict absolutely different conditions for northern high latitudes. They expect favourable conditions for temperate deciduous forest in Sweden, the shift of taiga into the present areas of tundra, in Siberia and in Alaska as well, the overall reduction of cold deciduous forest and tundra and the increase of cool mixed forest, cool conifer and taiga. Nevertheless, Claussen and Esch (1994) emphasize that due to a rapid climate change, their simulation is capable of predicting conditions favourable for

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certain biomes only, and not the future distribution of biomes. Little change is foreseen for tropical rain forests, for the Sahara as well as for warm grass and xerophytic woods south of it. However, favourable conditions for savannah are predicted to move into the Indian Desert. In South America, conditions favourable for xerophytic woods are found to spread southward, conditions for savannah shift southward in South Africa and Australia as well. Xerophytic woods are expected in France, too, whereas warm mixed forest may appear over the British Isles. Asian steppes may expand into southeast Europe.

In contrast to Claussen and Esch (1994), Kirilenko and Solomon (1998) conducted their simulation for different time slices. Wooded tundra, steppe and desert vegetation are predicted to begin to migrate during the first 50 years of simulation, while changes in forest vegetation appear first during years 50-100. Differing from other authors, Kirilenko and Solomon (1998) expect new, non-analogue forest biome types called "depauperate" (i.e. one plant functional type is missing) to emerge. These biomes are transitory but exist for a considerable amount of time, and appear in western Europe, eastern Asia and southeastern North America. A depauperate cool conifer forest biome (=southern taiga) appears at year 50, peaks at year 105 and then disappears by year 130. A depauperate temperate deciduous forest first appears 70 years into the simulation, reaches a peak cover at year 130 and slowly declines in area thereafter. A third unique biome, a depauperate cool mixed forest biome, is a minor component between years 60 and 130, with a peak at year 110. Immigration of forest vegetation is predicted to be the most significant between the years 200 and 500. While Claussen and Esch (1994) did not predict any important changes for tropical rain forest, Kirilenko and Solomon (1998) expect dry parts of tropical forests to be replaced by woodlands and savannahs during the first 100 years. According to the simulation, tropical forest immigration into newly available moist areas begins after the year 500. Kirilenko and Solomon (1998) took the rate of migration into account as well. In the case of average migration, plentiful transitory biome types are predicted to appear, and an initial loss of forests is foreseen. In the case of rapid migration, however, transitory biomes occupy just a few patches and for a much shorter time. Land use changes also influence vegetation changes to a great extent. When including agriculture in the simulations, fewer changes are expected in natural vegetation (due to less area), but these are considered to be fast. Just like Köhler et al. (2005), Kirilenko and Solomon (1998) also predict the dieback of trees (across large regions within a decade) and refer to recent forest diebacks in Europe, the Pacific Rim and northeastern North America (Mueller-Dombois, 1987; Auclair et al., 1990; Auclair, 1992). Regrowth by trees more suitable for new climates is doubtful and may take a century or more.

Development of no-analogue communities (communities that are compositionally unlike any found today) is predicted by Williams and Jackson (2007) as well. According to them, novel climates will arise by 2100, primarily in tropical and subtropical regions. These future climates will be warmer than any present climates globally, with spatially variable shifts in precipitation, and increase the risk of species reshuffling into future no-analogue communities and other ecological surprises. Since most ecological models are at least partially parameterized from modem observations, they may fail to accurately predict ecological responses to these novel climates.

Contrary to Claussen and Esch (1994), Levy (2004) mentions future reduction in rainfall in the Amazon basin and consequently a decline in the Amazonian forest areas.

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However, there is considerable uncertainty in this result since the decrease in precipitation is not reproduced in all GCMs.

Compared to the other authors, Yue et al. (2011) use a very detailed classification of biome types in their study, the Holdridge life zone model. As a consequence, much more vegetation types are mentioned. Simulations were conducted for three climate change scenarios (A1Fi, A2 and B2) and four intervals (1961-1990, 2010-2039, 2040-2069 and 2070-2099). Compared to the recent past, the following changes are predicted for the period 2070-2099: In all three scenarios, areas of subtropical moist forest, moist tundra and nival area would decrease. Under scenarios A2 and B2, subtropical dry forest would severely shrink as well. Areas of tropical dry forest, tropical very dry forest, tropical thorn woodland and cool temperate moist forest would have the biggest increase under all scenarios. This is in contrast with the results of Kirilenko and Solomon (1998), who found that dry parts of tropical forests would disappear. Desert areas would have a decreasing trend until 2039 and an increasing trend afterwards. Yue et al. (2011) also mention that ecological diversity would have a continuously decreasing trend under all three scenarios.

Contrary to others, Yue et al. (2011) identify which biome types will shift in which directions and in what extent. According to their predictions, subpolar/alpine moist tundra would shift towards west in the northern hemisphere under all scenarios. Mean centre of desert would move towards west because desert area would decrease in China and central Asia, however, Borborema plateau in Brazil would have a rapid desertification trend. Subtropical dry forest and warm temperate moist forest would shift towards northwest, and warm temperate wet forest and warm temperate thorn steppe towards northeast. Under scenarios A1Fi and B2, subpolar/alpine dry tundra would move towards west as well. In the southern hemisphere, the mean centre of warm temperate wet forest would shift towards southeast, cool temperate rain forest and warm temperate thorn steppe would move towards west, and cool temperate wet forest towards southwest under all three scenarios. Under scenarios A2 and B2, subtropical wet forest would move towards east. As a conclusion, all polar/nival, subpolar/alpine and cold ecosystem types would have a continuously decreasing trend. On the contrary, except tropical rain forest, all other tropical ecosystem types would increase. Subpolar/alpine moist tundra would be the most sensitive ecosystem type because its area would have the rapidest decreasing rate and its mean centre would shift the longest distance towards west.

Alo and Wang (2008) also examined the responses of global potential natural vegetation distribution to climate change. According to their simulations, vegetation response ranges from mild to rather dramatic changes of plant functional types. Although such response differs significantly across different GCM climate projections, a quite consistent spatial pattern emerges, characterized by a considerable poleward spread of temperate and boreal forests in the Northern Hemisphere high latitudes, and a substantial degradation of vegetation in the tropics (e.g. increase of drought deciduous trees coverage at the expense of evergreen trees), especially in western and southern Africa and South America. Despite this fact, net primary production is predicted to increase under most GCM scenarios over most of the globe. However, in some simulations extreme responses are shown in some regions: Deciduous forest is replaced by grasses in large areas in the middle latitudes, and substantial areas in northern South America and southern Africa predominantly covered by evergreen forest are replaced with grasses, while net primary production reduces drastically.

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Monserud et al. (1993) also used simulations to predict changes in global vegetation patterns. According to their results, the most stable areas are desert and ice/polar desert. Because most of the predicted warming is concentrated in the boreal and temperate zones, vegetation there is expected to undergo the greatest change. All boreal vegetation classes are predicted to shrink, while classes of tundra, taiga and temperate forest are predicted to replace much of their northern neighbours. Most vegetation classes in the subtropics and tropics are predicted to expand. Any shift in the tropics will be determined by the magnitude of the increased precipitation accompanying global warming. Monserud et al. (1993) are uncertain if projected global warming will result in drastic or minor vegetation change.

The same is confirmed by Neilson and Drapek (1998) as well, who think it is still under debate whether or not the world's vegetation will experience large drought-induced declines or perhaps large vegetation expansions in early stages. There may occur oscillations as well, perhaps on long timescales, between greener and drier phases. It may be that much of the world could become greener during the early phases of global warming, and reverse in later, more equilibrial stages.

Simulations by Salzmann et al. (2009) indicate a generally warmer and wetter climate, resulting in a northward shift of the taiga-tundra boundary and a spread of tropical savannahs and woodland in Africa and Australia at the expense of deserts. Salzmann et al. (2009) assume that changes in global temperature, and thus biome distributions, at higher atmospheric CO_2 levels will not have reached an equilibrium state by the end of this century.

Forests have been shown to respond strongly to many of the drivers which are predicted to change natural systems over this century, including climate, introduced species and other anthropogenic influences (McMahon et al., 2009). Kirilenko et al. (2000) limited their research to boreal forests of the northern hemisphere. They found that these forests would decline to a great extent and they would shift as well. As a consequence, the intersection between the current and future boreal forests zone would occupy only 9.5% of the current area. This reduction is not in line with the results of Claussen and Esch (1994). However, the predicted area decrease depends on the GCM outputs and conditions used for the simulations as well as on the predicted climate variability.

According to Klausmeyer and Shaw (2009), the Mediterranean biome is projected to experience the largest proportional loss of biodiversity of all terrestrial biomes by 2100. Climate change will impact the extent and distribution of the Mediterranean climate, posing a threat to the survival of many species. As the composition of Mediterranean vegetation differs among regions, the impacts on plant assemblages will differ as well. According to the majority of atmosphere-ocean general circulation models and emission scenarios, the Mediterranean climate extent at the end of the 21st century is projected to be larger than the current one. The median future Mediterranean climate extent will increase to 106, 107 or 111% of its current size, for the low, medium and high emissions scenarios, respectively. Some regions are predicted to experience an increase in the Mediterranean climate extent, such as the Mediterranean Basin and Chile/Argentina, while in some regions it is projected to decrease, such as in the United States/Mexico, South Africa and Australia. The majority of the contractions results from warming in winter or from a drop in total annual precipitation. Approximately 50% of the biome is projected to remain stable with confidence, even under the high emissions scenario. According to the IPCC, the Mediterranean biome as a whole is threatened by

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desertification from expansion of semi-arid and arid systems even under relatively minor warming and drying scenarios, and significant regional vegetation and species range shifts are predicted (Fischlin et al., 2007). Studies generally project significant reductions in endemic species range sizes (Phillips et al., 2008; Fitzpatrick et al., 2008; Gutierrez et al., 2008; Benito-Garzon et al., 2008; Loarie et al., 2008). For example, in California, 66% of the endemic plant taxa will experience > 80% range reductions within a century (Loarie et al., 2008), while Midgley et al. (2002) projected a 51-65% reduction in the Mediterranean biome in South Africa by 2050, and that only 5% of the endemic Proteaceae species modeled would retain more than two thirds of their current range. Fitzpatrick et al. (2008) studied potential range shifts for native *Banksia* species in Western Australia and found the areas of greatest percent loss in richness in the arid interior, while the projected loss was less severe in coastal areas. Native plant species in all Mediterranean regions, except perhaps Chile, are well adapted to natural fire regimes, but a hotter and drier climate has been observed to promote significant alterations to the fire regime (Pausas, 2004; Fischlin et al., 2007; Fried et al., 2004; Lenihan et al., 2003). Besides, the patchy nature of soils will act as a barrier and will make species migration more difficult. The intrinsic adaptation potential of some Mediterranean endemics, particularly in South Africa and Australia, is limited by the relatively short seed dispersal distances and lack of colonization ability of these plants (Fitzpatrick et al., 2008; Williams et al., 2005; Hammill et al., 1998; Schnurr et al., 2007).

Climate change induced vegetation shifts in Europe

Studies on the shift of vegetation zones in Europe are mainly limited to single countries. However, reviewing them gives a proper overview of the predicted changes in Europe.

The Alps and Switzerland

Plants from high-latitude and high-altitude sites appear to be sensitive to climate warming (e.g. Wookey et al., 1994, 1995; Parsons et al., 1994, 1995; Callaghan & Jonasson, 1995; Körner, 1999) since these are the regions where the highest temperature increases are expected. Mountain regions tend to warm more rapidly than the northern hemisphere average (Rebetez & Reinhard, 2008) and the rate of warming in mountains is expected to be up to three times higher than the global average rate of warming during the 20th century (Nogués-Bravo et al., 2007). That is why high mountain systems such as the Alps are likely to be particularly vulnerable to climate change (Beniston, 1994; Grabherr et al., 1994; Guisan et al., 1995; Beniston et al., 1996; Beniston et al., 1997; Kienast et al., 1998; Cebon et al., 1998; Theurillat & Guisan, 2001; Dirnböck et al., 2003). This sensitivity is especially important due to the fact that the Alps are one of the most important hot spots of endemic vascular plant species diversity in Europe (Myers et al., 2000; Aeschimann et al., 2004).

Over the last 20 years, several studies comparing recent survey data with historical data from the early 20th century documented an increase in species numbers on high mountain summits of the European Alps (Kammer et al., 2007). Frei et al. (2010) investigated 25 summits in the Swiss Alps and compared their results with data originating from the beginning of the 20th century (Rübel, 1912; Braun, 1913). They found a strong trend towards an increase in species richness per summit and also a

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significant increase in the mean number of summits colonized by each species during the 20th century. A mean upward shift of +145.3 m of the studied species was identified, which underlines the upward trend of upper range margins. However, there were a few species as well which descended to considerably lower areas. At the lower range limit, species at an altitude lower than 2,250 m showed a positive but non-significant upward trend, while species at higher altitudes than 2,250 m revealed a significant downward shift. When investigating both the upper and lower range margin shifts of the same species at the local scale, a more consistent upward shift was identified at the upper range limit, whereas at the lower range limit the pattern was more heterogeneous. As a conclusion, it can be stated that the majority of high alpine plants are moving uphill, but not all species are equally responsive. Although the increase in species richness on summits has more or less explicitly been attributed to anthropogenic climate warming, Kammer et al. (2007) state that suitable habitats already occurred on these summits under the mesoclimatic conditions prevailing at the beginning of the 20th century. Thus, they consider this phenomenon to be primarily the result of a natural dispersal process which was triggered by the temperature increase at the end of the Little Ice Age and which is still in progress mostly due to the dispersal limitation of the species involved. On the contrary, Walther et al. (2005) conclude that vegetation change and the upward shift of alpine plants have accelerated in the southeastern Swiss Alps since 1985, consistent with a climate change explanation. Due to the upward shift, there will be strong reductions in the area available for alpine species, resulting in a higher risk of local extinction of these species (phenomenon of “summit traps”, cf. Pertoldi & Bach, 2007; Guisan & Theurillat, 2000; Theurillat & Guisan, 2001). Very narrowly distributed endemics are especially vulnerable to climate change because of their smaller altitudinal distribution and the fewer number of colonized habitats (Ohlemüller et al., 2008). Dirnböck et al. (2003) also predict that range-restricted alpine endemics may face strong habitat reductions, as the tree line is only a few hundred meters below the isolated mountains tops. On the contrary, Scherrer and Korner (2011) expect that all but the species depending on the very coldest micro-habitats will find thermally suitable “escape” habitats within short distances, while there will be enhanced competition for the cooler places on a given slope in an alpine climate that is 2 K warmer. Due to their topographic variability, alpine landscapes seem to be safer places for most species than lowland terrain in a warming world (Scherrer & Korner, 2011).

However, not all species are able to track the changes of climate rapidly enough. On average, most alpine and nival species could tolerate the direct and indirect effects of an increase of 1-2 K (Körner, 1995; Theurillat, 1995), but not a much greater change, e.g. 3-4 K (Theurillat, 1995; Theurillat et al., 1998). According to Scherrer and Korner (2011), a 2 K warming will lead to the loss of the coldest habitats, the biggest part of the current thermal micro-habitats will be reduced in abundance (crowding effect) and a less part will become more abundant. Many isolated orophytes living in refugia such as the peaks of low mountains in the Alps would be threatened, because it would be almost impossible for them to migrate higher, either because they are unable to move there rapidly enough, or because the nival zone is absent (Grabherr et al., 1994, 1995; Gottfried et al., 1994). At the high alpine and nival belts, pioneer wind-dispersed species should be able to reach new sites at higher elevations (according to observations by Stöcklin & Bäumler, 1996). However, the speed of upward progression may not be rapid enough to keep pace with warming (Grabherr et al., 1994). Generally, species composition of the communities is determined by seed and site limitation jointly and

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constraining site factors include both abiotic conditions and biotic interactions (Dullinger & Hülber, 2011). In the Alps, natural dispersion is presently limited at lower elevation by forests, landscape fragmentation (roads, built-up areas) and changes in traditional agricultural land-use, such as abandonment of secular transhumance (Poschlod et al., 1998). In the alpine and nival belts, natural dispersion is limited mainly by natural (e.g. orographical, geomorphological, lithological) barriers.

As for Switzerland, an increase of 3.3 K in mean temperature, which corresponds to an altitudinal shift of 600 m, would reduce the area of the alpine vegetation belt by 63% on average (Theurillat & Guisan, 2001). The colline and montane vegetation belts would be reduced on average by 20% only and the subalpine vegetation belt by even less. When shifting upwards in elevation, species and communities would not find equivalent surface areas with similar physiographic conditions. According to Theurillat and Guisan (2001), the alpine belt will undergo the greatest change among all vegetation belts in Switzerland, since ca. one third of it will have an inclination greater than 40° instead of ca. one fifth at present. Consequently, this would lead to a marked decrease of communities bound to low inclination, like snowbed communities, some types of swards, alpine fens, mires and springs. In addition, the material of the layers (soft marl vs. hard limestone) and the variation in their sequence and thickness will play a role in the response of flora as well (Theurillat et al., 1998). Theurillat and Guisan (2001) predict that the current alpine belt would show a mosaic of subalpine and alpine elements. Part of the present high alpine vegetation would have to shift into the upper nival belt. For the tree line to expand upslope, it would be necessary for a significantly warmer climate to last for at least 100 years (Holtmeier, 1994a, b). Palynological and macro-fossil studies show that the forest limit did not climb more than 100-300 m during the warmest periods of the Holocene (e.g. Burga, 1988, 1991; Bortenschlager, 1993; Lang, 1993; Tinner et al., 1996; Wick & Tinner, 1997). An increase of 1-2 K in mean annual temperature may not shift the present forest limit upwards by much more than 100-200 m (Theurillat & Guisan, 2001). However, in the case of a temperature increase of 3-4 K, which is equal to the temperature range of an entire vegetation belt, the forest limit would very likely shift into the low alpine belt.

Díaz-Varela et al. (2010) studied the changes of timberline (forest limit), tree line (tree limit) and krummholz limit (crook-stem line, tree species limit or tree species line) in the Italian Alps and identified three vegetation classes: forest, patched/scattered trees and herbaceous tundra. They found that during the studied 49-year period, each land cover type increased its area at the expense of its immediate superior vegetation belt and only few cases of deforestation were recorded. The three ecotones showed a general trend to increase in altitude, retreats were far less common than advances. The forest, tree and tundra lines showed a net advance of 193, 78 and 92 m and medians of 124, 65 and 55 m respectively, which means, converted to decadal absolute increments, averages of 39, 16 and 19 m and medians of 25, 13 and 11 m for forest, tree and tundra shifts respectively. In the case of forest line and tundra line, the altitude advance magnitude decreased with the rise in altitude. An assessment of tree line for the entire Swiss Alps (Gehrig-Fasel et al., 2007) found a similar decadal increment of 23 and 18 m of mean and median altitudinal increment for a 12-year period. One record of temporal tree line dynamics on a slope in the Austrian central Alps (Wallentin et al., 2008) indicated a decadal advance of 28 m for the maximum elevation of tree line and 17 m for the mean elevation in the period 1954–2006. However, Nicolussi et al. (2005) provide far lower estimates of decadal altitudinal shift (less than 6 m) for tree line and

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tree species line in the central eastern Alps. Regarding tundra, Grabherr et al. (2001) assessed lower values in the central Alps (10 m/decade). Field experiments suggest as well that even moderate climate warming will cause an upland migration of alpine tundra and colonisation of the nival belt (Wagner & Reichegger, 1997; Theurillat & Guisan, 2001).

Gottfried et al. (1998) also confirm that the distribution pattern of individual plant species and that of plant communities is likely to be drastically affected by climate change at the alpine-nival ecotone. Plant migrations will be highly dependent on topographically determined gradients (Pauli et al., 1999). A general trend of decline of biodiversity was found with altitude, but with a maximum of species richness at the ecotone itself (Gottfried et al., 1998). Chionophilous plants at the scree sites may be affected severely by reduced snow cover (Pauli et al., 1999).

The shift of vegetation begins with changes in its composition. As for climatic climax communities, new plant communities are likely to develop and, partially or totally, replace present ones (e.g. Tallis, 1991; Theurillat et al., 1998). In the alpine belt, it is very likely that plant communities on moderate slopes (e.g. snowbeds with *Salix herbacea* and alpine swards with *Carex curvula*) would shrink or even disappear in some places. On the contrary, current edaphic climaxes could sustain a climatic change since azonal communities are assumed to be less sensitive to climate change (Kienast et al., 1998). According to Brzeziecki et al. (1995) and Kienast et al. (1995, 1996, 1998), 30-55% of the forest areas in Switzerland would show a change of classification types in the case of a temperature increase of 1-1.4 K and 55-89% with an increase of 2-2.8 K. According to several models (e.g. Fischlin et al., 1995; Fischlin & Gyalistras, 1997; Lischke et al., 1998; Kienast et al., 1995, 1996, 1997, 1998), montane forests dominated by deciduous trees would move toward a higher elevation, which would force subalpine coniferous forests to shift into the alpine belt. Some subalpine forests, such as the Arolla pine-larch forest (*Pinus cembra, Larix decidua*) in continental parts of Switzerland are predicted to show unexpected new tree combinations (e.g. Bugmann, 1999; Fischlin & Gyalistras, 1997). It is expected that beech-dominated forests (*Fagus sylvatica*) would be replaced by oak-hornbeam forests (*Quercus robur, Q. petraea, Carpinus betulus*) in the colline-submontane belt in the northern Alps; and an increase of silver fir (*Abies alba*) is predicted, from colline to low subalpine belt (Bugmann, 1999). In the southern Alps, changes are less likely to occur due to an increase in precipitation. However, the invasion by naturalized exotic laurophyllous species will replace the present tree layer (Gianoni et al., 1988; Klötzli et al., 1996; Walther, 1999, 2001; Carraro et al., 1999). The present Mediterranean-type vegetation in the warmest areas of the lowest elevations of the southern border of the Alps may very likely expand, while the colline downy oak forest (*Quercus pubescens*) may be severely affected by drought in the dry, continental part of the Alps (Theurillat & Guisan, 2001). With increasing risk of drought stress, laurophyllous species become less abundant and they are increasingly replaced by sclerophyllous, (sub)Mediterranean species (Berger & Walther, 2006). Walther (2003) reports that an exotic palm species, *Trachycarpus fortunei*, has successfully colonised the lower areas in southern Switzerland. Changing climatic conditions, especially milder winters and longer growing seasons, are assumed to have favoured the naturalisation of the palm and other exotic evergreen broad-leaved species, which dominate the understorey of the native deciduous forest in present times (Walther, 2003; Walther et al., 2007). According to Walther et al. (2007), palms are significant bioindicators for present-day climate change and their expansion is not driven by

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delayed population expansion. Increasing drought risk can lead to the collapse of forests in some areas as well (e.g. Bigler et al., 2006).

Kienast et al. (1998) took several climate change scenarios into consideration when studying possible changes of vegetation in Switzerland. As for the warmer and more xeric scenario, sample points were found to shift from montane beech-fir (Abieti-Fagion) communities to beech communities, while sample points in the colline/low montane belt are predicted to shift from Eu-Fagion to oak-hornbeam (Carpinion betuli) communities. For warmer and wetter conditions the vegetation shifts are less pronounced. In the case of moderate warming combined with wetter conditions, however, the responses of many vegetation types are even opposite to the warmer-more xeric scenario. Kienast et al. (1998) found a clear indication that communities of the current montane, high-montane and subalpine belt will lose area. Forests that occupy intermediate positions on the climatic gradient (e.g. *Fagus* forests) are predicted to expand into higher locations, however, topographic constraints will limit their dispersal. The overall "winners" of a warming without precipitation increase are vegetation types of the current colline belt (Carpinion-betuli, Quercion pubescenti-petraeae, Quercion robori-petraeae) as well as colline communities that are not present within the borders of Switzerland but in more xeric parts of the Mediterranean area. These results are in line with those of Theurillat and Guisan (2001). The shift from high montane or subalpine communities to low montane communities results in an increasing species richness as well.

Didion et al. (2011) investigated the effects of climate change and grazing on vegetation in three valleys in the Swiss Alps. They found that climate change led to an upslope shift of species (by approximately 1000 m) and of the cold treeline. The current forest types (dominated by *Picea abies*) were substituted by deciduous trees (*Fagus sylvatica* and *Castanea sativa*, respectively) in the valley bottom in the valleys with moist and wet climate and by non-forest vegetation in the dry valley. Simulated climate change resulted in the formation of new forest types, dominated by *Tilia cordata* and *Quercus* spp., as well. In all sites, browsing pressure led to a reduction of the abundance of *Abies alba* and *Fagus sylvatica*, while some browsing-sensitive but more light-demanding species such as *Pinus cembra* and *Quercus* spp. did not suffer significantly. When simulating the combined effects of climate change and ungulate browsing, it was found that browsing partially counteracted the effects of climate change, e.g. by retarding forest development at the cold treeline on the north-facing slope by several decades, but it amplified the effects of climate change in other plots, e.g. by exacerbating the collapse of forests near the dry treeline. On the south-facing slope, the current subalpine *Larix decidua-Pinus cembra* forest was replaced by a *Quercus spp.-Pinus sylvestris* forest over several centuries while *Pinus cembra* was gradually replaced by new species.

Studying subalpine grasslands in the Swiss Alps, Vittoz et al. (2009) found that these habitats were stable with smaller changes. Only a few species appeared or disappeared and changes were generally limited to increasing or decreasing frequency and cover of certain taxa. Declining species were predominantly alpine and low-growing species and their decline was probably due to increased competition with more vigorous subalpine taxa no longer limited by grazing. Thus, changes in these communities were mainly driven by changes in land management due to global warming. These results are in line with those of Dullinger et al. (2003), who also confirmed that range shifts of tree and shrub species in the European Alps are caused by land use change as well. Dullinger et

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al. (2003) conclude that colonization success strongly depends on propagule pressure and differential invasibility of grassland types but only marginally on local-scale site conditions. In a particularly invasible grassland type, a possible climate change-driven upward movement of *Pinus mugo* shrublands may take place quite rapidly. In contrast, encroachment on abandoned subalpine pastures is frequently delayed by competition with vigorous grassland canopies.

In France, species widely distributed in Provence, such as Scots pine, may be replaced by other Mediterranean species such as Aleppo pine (*Pinus halepensis*) (Martinelli, 2004). Chauchard et al. (2010) found that in parts of the French Alps *Abies alba* extended its range upslope by about 300 m during the last five decades.

Scandinavia

In northern Scandinavia, temperatures now may be higher than at any time in the past 4000-5000 years (Kullman & Kjallgren, 2000; Kullman 2000a). A general trend of summer warming could be observed and winters have been consistently milder (Kullman, 2002). Mean annual precipitation has increased throughout the 20th century.

Global warming at an unprecedented rate (Houghton et al., 1996) will force upward movement of altitudinal range-margins of plant species and bioclimatic zones by 400-600 m over the next 100 years (Boer et al., 1990; Holten & Carey, 1992; Grace, 1997).

Koca et al. (2006) studied vegetation changes in Sweden using different climate scenarios and predict the extension of the boreal forest northward and to higher elevations, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) joining mountain birch (*Betula pubescens ssp. czerepanovii*) at a higher alpine tree line. Pine and spruce are expected to remain the dominant species in the boreal zone, however, a shift in dominance from Scots pine to deciduous broadleaved trees, lime (*Tilia sp.*), silver birch (*Betula pendula*) and oak (*Quercus sp.*) is predicted for the Baltic coast and the central boreal region. Similarly, in the boreo-nemoral zone the dominance of spruce and pine will be reduced in favour of deciduous species, especially beech (*Fagus sp.*) and lime. The northern boundary of this zone is expected to be displaced northwards. However, these simulations ignored dispersal limitations as well as anthropogenic effects such as land use or silvicultural management so the rate of change in tree species distributions may be overestimated.

Kullman (2002) studied range-margin displacements of some tree and shrub species over the past 50 years. In the case of *Betula pubescens ssp. tortuosa*, he identified an advancement of the range-margin amounting to 315 m and thus the rise of the local tree limit by some tens of metres in the recent past. As for *Sorbus aucuparia*, the range-margin was found 375 m higher, while that of *Picea abies* 240 m higher. The present-day range-margin of *Pinus sylvestris* is 340 m higher than in the 1950s. In the case of *Salix* species, a range margin rise of 120-165 m has taken place. Besides, a new species, *Acer platanoides* has appeared, which is not native to that part of Sweden. Other non-native tree species, e.g. *Pinus contorta* and *Pinus cembra*, have also become established in similar environments elsewhere in the Scandes (Kullman, 2000b). Based on these observations, range-margin rise and invasion into alpine tundra communities, high above the current tree-limits, are foreseen for many tree and shrub species. This is supported by the tree-limit and range-margin rise amounting to 100-150 m identified over the past century more generally in the study region (Kullman, 2000a, 2001). Kullman (2006) estimates a treeline advance of 75-130 m since the early 20th century, depending on species and site. Young saplings of all tree species have appeared

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growing 400-700 m atop of the treeline and subalpine/alpine plant species have shifted upslope by average 200 m (Kullman, 2006). Kullman (2006) assumes that many plants adjust their altitudinal ranges to new climatic regimes much faster than generally assumed, however, plants have migrated upslope with widely different rates. Besides, a reversal of this trend was recorded as well during some colder decades (Kullman, 1997), which proves the great responsiveness of tree-limit vegetation to climate variability. Furthermore, a warmer climate regime might facilitate rapid spread of exotic tree species into natural ecosystems, whose character may become substantially altered (e.g. Beerling & Woodward, 1994; Sykes, 2001). This is in line with the observations in the Alps (Theurillat & Guisan, 2001). Thus, changes in the composition of vegetation are expected to occur and future subalpine and alpine plant cover is likely, at least transiently, to contain communities without previous analogues (Davis, 1989), i.e. mixtures of alpine and silvine species (Kullman, 2006). As a consequence, the character of the remaining alpine vegetation landscape is changing, for example, extensive alpine grasslands are replacing snow bed plant communities (Kullman, 2006). However, the observed processes will not inevitably lead to tree-limit advance and afforestation up to the level of the new range-margins since this would probably presuppose much warmer summers and substantially reduced wind pressure (Kullman, 2002).

Klanderud and Totland (2005) studied the effects of simulated climate change on the dwarf shrub *Dryas octopetala* (mountain avens) in alpine Norway. They found that some years of experimental warming had no effect on the cover of this species. However, in treatments with nutrient addition and with warming combined with nutrient addition, the cover of *Dryas* decreased while the biomass of the community significantly increased due to increased richness and abundances of graminoids and forbs. Lichen diversity and bryophyte richness became higher in treatments with only warming, while they decreased in treatments with only nutrient addition. Thus, climate change simulations resulted in the change of dominance hierarchies and community structure: *Dryas* was replaced by graminoids and forbs in plots with nutrient addition and mainly by graminoids in plots with warming combined with nutrient addition, and the heath changed to a meadow. In another experiment, Klanderud (2008) arrived at similar conclusions. Warming alone decreased the abundance of some *Carex* and bryophyte species, but did not affect community composition. In contrast, nutrient addition and warming combined with nutrient addition increased the abundance of high stature species, such as grasses and some forbs, while low stature forbs, a lycophyte and most bryophytes and lichens decreased in abundance. After four years of warming combined with nutrient addition, community composition changed significantly, suggesting that tall species may expand at the expense of low stature species in the alpine region.

Molau and Alatalo (1998) found in subarctic-alpine plant communities that the responses to temperature and nutrient treatments differed among mosses, lichens, vascular plants, and communities, and that climate change may cause a shift in the bottom layer from being dominated by mosses, to become dominated by lichens.

Wiedermann et al. (2007) studied vegetation responses in a boreal mire and found them negligible for the first four years of experiments. However, after eight years, the closed *Sphagnum* carpet was drastically reduced and total vascular plant cover (graminoid and dwarf-shrub species) increased. Thus, the study demonstrates that both bryophytes and vascular plants at boreal mires exhibit a time lag of more than five years in response to nitrogen and temperature rise. The slow and gradual shift from *Sphagnum*

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to vascular plant dominance was shown in another study as well (Wiedermann et al., 2009).

Snow regimes are also altered by climate change. Kreyling et al. (2012) showed in an experiment conducted in a boreal *Picea abies* forest that understory species composition was strongly altered by snow cover manipulations and vegetation cover, in particular the dominant dwarf shrub *Vaccinium myrtillus* (bilberry) and the most abundant mosses, significantly declined in the snow removal treatment. As a conclusion, shifts are caused in vegetation by frost damage as well.

Western Europe

In Europe, forest transformation from Norway spruce (*Picea abies*) to European beech (*Fagus sylvatica*) is already ongoing on a large scale (Spiecker et al., 2004) and Norway spruce is predicted to be one of the big "losers" of climate change. Thuiller (2007) estimated that each 1 °C of temperature change moves ecological zones on Earth by about 160 km in a North–South direction. From 1987 to 2002 the area of Norway spruce decreased from more than 42% of the total forest area to 36% in Germany (BMELV, 2005). According to model predictions, Norway spruce will be pushed back to the highest elevations in Baden-Württemberg in the southwest (Black Forest area) and the east (Swabian Alb and pre-Alps) of the state (Hanewinkel et al., 2010). In the year 2100 it will be restricted to forest areas distinctly above 1000 m a.s.l. and existing stands will be reduced by 20-38%. Potential growth area is expected to decrease drastically, only 5-28% of the total forest area in Southwest Germany is assumed to be suitable for growing Norway spruce in 2100.

Lasch et al. (2002) conducted their research in Brandenburg state in Germany. According to model simulations, abundance of beech will decrease significantly with increasing temperature (> 1.5 K) and most forests will be composed of drought tolerant species such as pine (*Pinus sp.*), oak (*Quercus sp.*), hornbeam (*Carpinus sp.*) and lime (*Tilia sp.*). Lasch et al. (2002) studied the effects of potential climate change on managed forests as well and found that the dominant role of pine forests was preserved in the simulations, however, beech disappeared completely.

Lenoir et al. (2010) assessed changes in plant community composition between 1989 and 2007 by surveying *Abies alba* (silver fir) forest vegetation releves in the Jura Mountains. Although temperature and light availability increased in these stands, no major changes in overall species distribution were found (only a trend towards a greater frequency of lowland species), perhaps reflecting dispersal limitation, phenotypic plasticity or microclimatic buffering by the tree canopy. In a previous study on European tree taxa (Lenoir et al., 2009), it was found that records of the mean altitude of presence at the seedling life stage are higher than those at the adult life stage. This trend suggests a main driver of change highly related to elevation, such as climate warming.

Van der Veken et al. (2004) conducted their research in Querco-Fagetea forests in France, Belgium and the Netherlands. They found that the expected increase of 3 °C in the northern part of the study area will cause several forest plant species to move several hundreds of kilometers northward and to thereby change present-day community structures. Scleromorphic species, hemicryptophytes and stress-tolerant species are expected to become relatively more abundant in the northern regions of the study area, and many species might have a chance to become vulnerable to extinction.

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Wessel et al. (2004) compared European shrublands in their study: lowland dry heathlands in the Netherlands and in Denmark as well as an upland heathland in the United Kingdom. In the warming treatment there was in increase in primary production in all three sites. If nutrient availability increases as a result of global warming, grasslands may replace heathlands since grasses have an advantage over heather under richer nutrient conditions (Heil & Aerts, 1993; Diemont, 1996). This is in line with the results of Klanderud and Totland (2005) in Norway. In drought treatments productivity and nutrient cycling decreased, thus, in this case heather (*Calluna sp.*) would be better able to compete with grasses. However, increased drought and herbivory damage could also be fatal for heather plants, creating gaps in the canopy and thus promoting invasion by grasses.

Breeuwer et al. (2009) investigated the effects of decreased summer water table depth on peatland vegetation in the Netherlands and found that increased water table drawdown affected the composition of the vascular plant vegetation, stimulating the abundance of ericoid species. Increased occurrence of periods with low water tables, due to climate change, may cause a shift in the dominant *Sphagnum* (peat moss) species. On the transition between hollows and lawns, the species assemblage is expected to shift from vegetation dominated by hollow Sphagna (e.g. *Sphagnum cuspidatum*) and graminoids, to vegetation dominated by lawn Sphagna (e.g. *Sphagnum magellanicum*) and ericoids.

Walmsley et al. (2007) predict that the increase in air temperatures and changes in precipitation patterns projected for the 21st century (Hulme et al., 2002) are likely to have profound consequences for community composition and structure and ecosystem processes across the UK. According to Higgins and Schneider (2005), biological communities in the North Atlantic region could be heavily influenced by the collapse of the thermohaline circulation. It poses a threat to the remnant habitat fragments, upon which much of England's remaining biodiversity depends, by causing shifts away from the currently dominant temperate broadleaf cold deciduous tree type.

Beech (*Fagus sylvatica*) has been identified in Britain as potentially sensitive to the effects of climate change because of its sensitivity to summer drought (Peterken & Mountford, 1998). Beech may show a significant expansion northward and westward (towards the wetter coast) (Harrison et al., 2001), although other models indicate limitations on westward expansion due to inadequate chilling conditions (Sykes et al., 1996). According to Broadmeadow et al. (2005), beech is not likely to disappear from southern England, but its yield potential is expected to fall and its competitive ability is therefore likely to change. Wesche et al. (2006) state that it is unlikely that woodland specialist species would be able to migrate from southern England to northern woodlands since these are relatively poor colonisers (Peterken, 1974; Hermy et al., 1999) and woodland cover in Britain is highly fragmented. However, assemblages similar to southern beech woodlands may develop if common species in the South already occur in woods in the North and West. As species respond individualistically to changing environmental conditions, plant communities will not move en masse and new communities in the Northwest will not be exactly the same as those in the Southeast. Climate change will affect the distribution of woodland ground flora independently of beech.

Del Barrio et al. (2006) studied two habitats in East Anglia, cereal field margins and lowland calcareous grassland. Results of model simulations show that among the studied species, *Campanula glomerata* (clustered bellflower) will lose climate space

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from Scotland, but gain in Wales and western England. *Helictotrichon pratense* (meadow oat-grass) will spread westwards, but by 2080 the distribution becomes quite fragmented with large losses in southern and eastern England and in Scotland, respectively. As for the species associated with cereal field margins, climate space will increase for *Silene gallica* (small-flowered catchfly) and *Papaver dubium* (long-headed poppy). Land use change scenarios suggest fairly large reductions in arable land use classes, thus suitability is expected to decrease significantly for the cereal field margin species. Del Barrio et al. (2006) state that climate change may not involve a zonal shift of natural vegetation, but instead gaps may open within the current vegetation zones and they may be colonised by low quality, early successional species. Complete replacements can be expected to be very slow. At the regional scale climate and land use change can both affect the future viability of species.

In a long-term experiment conducted in an unproductive, grazed grassland in northern England, Grime et al. (2008) observed that the relative abundance of growth forms was constant and long-lived, slow-growing grasses, sedges and small forbs remained dominant. Several species remained stable over the course of the experiment, with immediate but minor shifts in their abundance. No change in productivity in response to climate treatments was detected with the exception of reduction from summer drought; and only minor species losses were observed in response to drought and winter heating. Overall, compositional changes were less than short-term fluctuations in species abundances. Grime et al. (2008) concluded that unproductive ecosystems provide a refuge for many threatened plants, and changing land use and over-exploitation rather than climate change per se constitute the primary threats to these fragile ecosystems.

McGovern et al. (2011) resurveyed an upland Agrostis-Festuca grassland in 2008, 40 years after the original survey. A significant shift in community composition was found, reduction in species richness and an increase in the grass:forb ratio, suggesting significant ecosystem degradation. However, the main shifts in species composition were correlated with an increase in pH, and clear ecosystem responses to climate, land-use change or nitrogen enrichment were not observed.

In an experiment in the effects of climate change on heather (*Calluna sp.*) and bracken (*Pteridium sp.*), Werkman and Callaghan (2002) observed that biomass of deciduous bracken fronds was significantly increased by higher growing temperatures, while additional N had little effect. Overall, bracken is likely to benefit from the currently rising temperatures in Britain. In contrast, direct effects of the temperature and N treatments on heather were small, but it showed considerable reductions in vigour in the boundary plots. Thus, heather is expected to be further displaced by bracken in a warmer climate.

Studying heathland vegetation in Scotland, Crabtree et al. (2010) found that with the upward shift of vegetation zones due to warming, suitable habitat for alpine lichens was reduced. However, decreasing wind speed exaggerates the effects of increased temperature and vice versa. An increase in mean wind speed may negate the effect of increased temperature on vegetation structure, resulting in no net change in lichen occurrence.

Studying grasslands in Germany, Buetof et al. (2012) observed that simulated climate change had a general negative effect on plant survival and plant growth, irrespective of the macroclimatic niche characteristics of the species, and species with

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ranges extending into drier regions did not generally perform better under drier conditions. Growth performance and survival varied according to land-use types.

Duckworth et al. (2000) studied calcareous grasslands in Britain, Ireland, France and Spain, and concluded that a 2 °C increase in temperature may cause small shifts towards vegetation associated with warmer conditions, representing distances of 100 km or less. The potential for major change is lower when environmental factors such as soil and management are considered in addition to climate and when vegetation is considered as a whole rather than on an individual species basis, due to both interspecific interactions and interactions with environmental factors acting as constraints.

Southern Europe

In Mediterranean-type ecosystems decreased water availability caused by high summer temperatures and low rainfall is already the most important environmental constraint (Specht et al., 1983; Larcher, 2000; Le Houerou, 2005; Savo et al., 2012). Global circulation and regional models predict an increase in temperature in the Mediterranean Basin during the present century, while rainfall is predicted to decrease and become more irregular (Gibelin & Déqué, 2003; Sánchez et al., 2004). Therefore this region is expected to be extremely vulnerable to climate change (Schröter et al., 2005), although the Mediterranean flora is particularly adapted to frequent and severe stresses (Vennetier & Ripert, 2009). With increasing temperatures, many species have already shifted their ranges to more suitable habitats, moving upwards in elevation or towards the poles (Hughes, 2000; Lenoir et al., 2008), particularly in mountains and at high elevation (Walther et al., 2005). The expected shift in the 21st century (Thuiller, 2004) is faster than tree species spread recorded at the end of the last ice age (Delacourt & Delacourt, 1987) and than the sprawling of most invasive plants monitored today (Richardson & Rejmanek, 2004). Malcolm et al. (2006) forecast high rates of potential extinction among endemic species (average 11%, up to 43%) for the whole Mediterranean basin and other biodiversity hotspots in the world by 2100. Many remnants of alpine or medio-European flora, located at the limit of their distribution range and protected in Mediterranean mountain reserves, should be the first to disappear (Vennetier & Ripert, 2009). The extensive dieback of some dominant tree species like Scots pine (*Pinus sylvestris*) in the French Mediterranean area (Vennetier et al., 2008) also suggests that the most mesophilous species are really at risk in these regions.

Vennetier and Ripert (2009) simulated the turnover in the flora in Mediterranean forests in Southeastern France and found that a 20% reduction of spring or summer rainfall would correspond to a 4-5% turnover (i.e. only 1 plant species, rarely 2, would change among 25). An increase of 1 °C would cause a 7% turnover, and combined with a 10% loss of spring or summer rainfall it could change 10% of the plant composition. The average climate of respectively the last 30, 20 and 10 years led to a potential 11.5%, 14% and 25% plant species turnover. In field studies they observed that 50% of mesophilous plant species lost ground between 1998 and 2008, disappearing from plots, far more than among the super xero-thermophilous ones (only 20%). On the opposite, only 10% of the mesophilous plants were found in new plots compared with 40% of the super xero-thermophilous plants. Some super xero-thermophilous and xero-thermophilous species, already present in 1998, increased in dominance and cover. Vennetier and Ripert (2009) assume that the adaptation time of plant composition to the current climate change is close to 20 years in the study area. *Quercus pubescens* (downy

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oak) limit is predicted to move away from the coast, thus high rates of dieback are expected, leading to an increased fire risk due to dead fuel accumulation.

Di Traglia et al. (2011) simulated potential distribution changes of tree species in Italy. *Abies alba* (silver fir) is expected not to completely disappear from the central and south Apennines, however, distribution area of *Pinus sylvstris* and *Fagus sylvatica* (European beech) will be strongly reduced. An exception to this general behaviour is given by *Acer campestre* (field maple) and *Quercus suber* (cork oak), belonging to sub-Mediterranean and Mediterranean choro-types, respectively. These two species show an increase of abundance values and distribution area for one of the scenarios but a reduction under a more limiting scenario. The enlargement of the potential area of *Quercus suber* is accompanied by a parallel decrease of *Quercus ilex* (holm oak) (Attorre et al., 2011), which is more sensitive to the reduction of soil moisture content (Ogaya & Peñuelas, 2003) caused by climate change especially in the southern part of Italy and along coastal areas. Di Traglia et al. (2011) predict the overall decrease of forest cover (with some exceptions), mainly due to increasing aridity and risk of drought (Andreu et al., 2007; Macias et al., 2006). Thus, significant rearrangements of forest communities are expected on the Italian peninsula.

In Greece, Fyllas and Troumbis (2009) identified fire to play a significant role in low-altitude sites. In their simulations, its significance increased with the severity of the climate change scenario, suggesting a greater vulnerability of mountainous Mediterranean drier areas regarding compositional alteration and flammability trends.

Gritti et al. (2006) simulated vegetation dynamics on five of the main islands of the Mediterranean Basin: Mallorca, Corsica, Sardinia, Crete and Lesvos. According to their results, the effect of climate change alone is likely to be negligible in many of the simulated ecosystems. The simulated progression of invasion was highly dependent on the initial ecosystem composition and local environmental conditions, with a particular contrast between drier and wetter parts of the Mediterranean, and between mountain and coastal areas. Thus, the rate of ecosystem disturbance was the main factor controlling susceptibility to invasion. Gritti et al. (2006) concluded that further invasion into Mediterranean island ecosystems is likely to be an increasing problem, and in the longer term, almost all the ecosystems will be dominated by exotic plants irrespective of disturbance rates.

Wessel et al. (2004) compared different European shrublands in their study. For the experimental plot in Spain they found that net primary productivity was unchanged in the warming treatment (Peñuelas et al., 2004), and seedling recruitment of the shrubs (*Erica multiflora* and *Globularia alypum*) decreased, while that of the half-shrubs (*Fumana ericoides*, *Fumana thymifoli* and *Coris montspelliensis*) increased (Lloret et al., 2004; Peñuelas et al., 2004). In the drought treatment, plant primary productivity was reduced (Peñuelas et al., 2004), and the seedling recruitment shifted from shrubs to half-shrubs, just like in the warming treatment (Lloret et al., 2004; Peñuelas et al., 2004). This confirms that warming and drought may induce a shift in the composition of the plant community.

Lloret et al. (2009) also studied a shrubland in Spain and conducted drought and warming treatments. Their results show that drought treatment induced significant changes in the species composition of seedlings and a decrease in seedling density, whereas warming treatment did not produce relevant changes. Nevertheless, species responded differently, e.g. the dwarf shrubs *Fumana ericoides* and *Fumana thymifolia* and the shrub *Rosmarinus officinalis* were less negatively affected. *Globularia alypum*

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establishment was seriously reduced by drought, however, adults were less sensitive. Generally, it could be observed that the adult species composition of plots with different treatments did not change significantly, thus in many species the dynamics of adults did not correspond with the patterns observed in the case of their seedlings. Since perennial grasses did not increase with treatments, it can be assumed that drought may enhance less structured shrublands, but not necessarily a replacement by grasslands.

Del Barrio et al. (2006) simulated the potential distribution of some plant species in Spain. They observed general increases in climatic suitability for two species, *Chamaerops humilis* (European fan palm) and *Pistacia lentiscus* (mastic). Areas of high elevation gradually become suitable for these species, however, suitability will be lost in the south of the region by 2080 for *Pistacia lentiscus* according to one of the scenarios. As *Chamaerops humilis* is a thermophilous species, the predicted warming will increase its potential distribution area. *Pinus halepensis* (Aleppo pine) shows a small increase in suitability in the mountainous parts of the study region, but loses climate space in the south. Other three species, *Pinus pinaster* (maritime pine), *Quercus ilex* (holm oak) and *Quercus faginea* (Portuguese oak) show a general decrease in climatic suitability. Current distribution area of *Quercus ilex* remains within areas of suitable climate up to 2080, however, that of *Pinus pinaster* will be classified as climatically unsuitable by 2050, while climate space of *Quercus faginea* is expected to show a large decrease in 2080. For *Quercus ilex* and other montane species core areas of suitability are centred more and more on the top of mountains, and for this reason the impact of climate change for them is probably stronger in terms of loss of connectivity than in terms of loss of potential space.

Temperature increases and variations in rainfall patterns can profoundly alter the dynamics of drought-sensitive tree species in the Mediterranean mountain forests (Macias et al., 2006; Sarris et al., 2007, 2010; Peñuelas et al., 2007; Andreu et al., 2007). The southernmost European mountain forests in Andalusia (Spain) are perhaps among the most vulnerable areas for the loss of tree species due to climate change (Linares & Tíscar, 2011b). Several studies focusing on the Iberian Mediterranean mountains have reported declining tree-growth trends related to temperature rise and drought (Jump et al., 2006; Macias et al., 2006; Andreu et al., 2007; Sarris et al., 2007, 2010; Martínez-Vilalta et al., 2008; Piovesan et al., 2008; Galiano et al., 2010; Linares et al., 2011a).

Linares and Tíscar (2011b) conducted their study in the southern distribution area of *Pinus nigra ssp. salzmannii* (Pyrenean pine), a drought-sensitive Mediterranean mountain pine (Linares & Tíscar, 2010). There was a significant increase in mean annual temperature in the study area between 1799–2004, mainly due to 20th century warming, where spring and winter registered the greatest temperature increase. Annual precipitation showed significant negative trends, with the greatest precipitation decrease in spring. Linares and Tíscar (2011b) found that since the beginning of the 20th century, Pyrenean pine stands from drier sites showed declining growth trends, which were significantly more pronounced for warmer stands. According to their results, wet and dry stands follow contrasting growth trends, characterised by steady-to-rising basal-area increments in the wetter stands and declining basal-area increments in the drier ones. This supports the assumption that species responses to climate are not uniform over space (Miyamoto et al., 2010; Galiano et al., 2010; Sarris et al., 2010). For *Pinus nigra*, the capacity to adapt to climate change will likely vary across rainfall gradients as long-term growth responses to climatic change are linked to local mean precipitation. For

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drier and warmer sites, impending *Pinus nigra* decline and progressive replacement by better drought-adapted Mediterranean taxa could be expected (Linares & Tíscar, 2011b).

As the climate of the Mediterranean basin is becoming warmer and drier (IPCC, 2007), an increase in drought-induced mortality of Scots pine (*Pinus sylvestris*) has been predicted as well (Martínez-Vilalta & Piñol, 2002). Changes in the recruitment pattern may promote shifts in species composition and in distribution areas in response to drought episodes (Galiano et al., 2010). Studying a Scots pine forest in Spain, Galiano et al. (2010) found that increasing defoliation and mortality were associated with lower summer water availability and higher stand density. *Quercus humilis* (downy oak) and *Quercus ilex* had higher recruitment rates in the study area supporting the fact that seedlings of *Quercus* species have a competitive advantage over Scots pine under drought stress conditions (Marañón et al., 2004). In the midterm, this could result in a vegetation shift in the study area, from pine dominated to broadleaf dominated forests. As a consequence, many rear-edge populations of Scots pine sheltered in the mountain environments of the Iberian Peninsula could be at risk under future climate scenarios.

During the last three decades, Scots pine forests distributed in dry sites were most affected by fire (Vila-Cabrera et al., 2012). Vulnerability of these forests to fire is increasing in Spain and almost no regeneration could be observed after crown fires, due to a limited capacity to recolonize from unburned edges. Oak (*Quercus sp.*) forests, shrublands and mixed resprouter forests are predicted to replace burned Scots pine forests. Thus, increased vulnerability to fire of Scots pine forests under future, warmer conditions may result in vegetation shifts at the southern edge of the distribution of the species.

García-Romero et al. (2010) also conducted their research in the Mediterranean mountains in Spain. According to their results, vegetation with a high nival correlation (i.e. nival herbaceous vegetation and wet grassland) reduced significantly between 1957–1998. Likewise, vegetation with a moderate nival correlation (i.e. rocky-outcrop herbaceous vegetation, psychroxerophilic grassland and open and sparse broom shrublands) and vegetation with a low nival correlation (i.e. block-field herbaceous vegetation, open juniper and juniper/broom shrublands and dense juniper and juniper/broom shrublands) also lost area. On the contrary, vegetation with a negative nival correlation (i.e. psychroxerophilic grassland with broom and juniper shrubs, sparse broom/juniper shrubland and dense broom shrubland) expanded noticeably. In fact, a series of successional changes lead to the replacement of the vegetation, i.e. nival herbaceous vegetation and wet grasslands were replaced by a sparse broom shrubland (*Cytisus carpetanus*), which became steadily denser until it was replaced, first by an open shrubland and then by a denser one. García-Romero et al. (2010) found that vegetation changes were induced by changes in temperature, rainfall volumes and snow distribution and duration.

By comparing current and 1945 vegetation distribution in Northeastern Spain, Peñuelas et al. (2003, 2007) observed a progressive replacement of cold-temperate ecosystems by Mediterranean ecosystems. Beech (*Fagus sylvatica*) forest has shifted upwards by ca. 70 m at the highest altitudes (1600-1700 m). Both beech forests and heather (*Calluna vulgaris*) heathlands are being replaced by holm oak (*Quercus ilex*) forest at medium altitudes (800-1400 m), which occurs through a progressive isolation and degradation of beech stands. The replacement is caused by progressively warmer

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conditions, complemented by land use changes (mainly the cessation of traditional land management).

In the North of Spain, a more oceanic climate can be expected, leading to an increase in territories having a temperate climate (del Rio et al., 2005). Thus, deciduous forests could increase their distribution limits, replacing some semi-deciduous and evergreen ones.

Sanz-Elorza et al. (2003) found significant changes in vegetation on the high summits of the Spanish Central Range over the period 1957–1991. A shift towards warmer conditions could be observed since the 1940s, with significantly higher minimum and maximum temperatures, fewer days with snow cover and a redistribution of monthly rainfall. High-mountain grassland communities dominated by *Festuca aragonensis* were replaced by shrub patches of *Juniperus communis ssp. alpina* and *Cytisus oromediterraneus* from lower altitudes. Sanz-Elorza et al. (2003) hypothesize that the advance of woody species into higher altitudes is probably related to climate change, in conjunction with variations in landscape management.

Sebastia (2007) states that subalpine grasslands in the Pyrenees are considered to be especially vulnerable to climate change because of their position at the south-western edge of the semi-natural grassland biome in Europe. Experiments showed that biomass production was more temperature-limited than water-limited in these communities. Grasses were dominant at high resource levels, while forbs dominated the community when water and nutrients decreased. The effect of increased biomass with decreased water was related to shifts in dominance from grasses to forbs, probably enabled by decreased nutrient availability under drought conditions. Sebastia (2007) concluded that the capability of high-altitude grasslands to provide quality forage in summer time could be threatened in the northern Mediterranean region under climate change conditions. In another study in mesic grassland ecosystems in the Pyrenees, Sebastia et al. (2008) observed strong shifts in plant diversity and composition after a short period of warming and drought, as a consequence of acute vulnerability of some dominant grasses and losses of rare species. The most dominant species, *Festuca nigrescens* (alpine chewing's fescue), reduced its abundance significantly.

Studying wet grasslands in Bulgaria, Hájek et al. (2008) found that climate change could cause deterioration of high-altitude wet grasslands, which are rich in local endemics, and observed the upward shift of Central-European vegetation types.

Central Europe

In Slovenia, Kutnar and Kobler (2011) predict that the share of vegetation types will be altered under the impacts of climate change, and the shift of vegetation belts upwards might be expected. By the year 2100, the share of mesic beech forests (*Fagus sp.*) and that of Dinaric fir (*Abies alba*)-beech forests is likely to decrease. Furthermore, a significant increase of the share of thermophilous forests is expected and a significant part of the coniferous forest with *Picea abies* (Norway spruce) and *Abies alba* predominating might be converted to deciduous forests.

Svajda et al. (2011) reported the upward shift of the tree line in the western Tatras, in Slovakia. The distribution of dwarf pine *(Pinus mugo*) and the percentage of total surface area covered by it systematically increased from 1965 to 2002 on all monitored sites.

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Russia

According to the IPCC reports (2001, 2007), East Eurasia is a region with strong climate changes in both temperature and precipitation. The greatest temperature anomalies are found in the Northern Hemisphere high latitudes and the warming is particularly strong in winter and spring (Serreze et al., 2000; Groisman et al., 2006). In West Siberia, the annual temperature has increased 1 °C, in the southern Urals, winter temperatures have risen 0.6-1.1 °C over the last 20-30 years, and in central Siberia and central Yakutia, winter temperatures have risen 2-4 °C and 3-10 °C, respectively (Tchebakova & Parfenova, 2006). Tchebakova et al. (2011) found a larger winter warming in the north; conversely, summer warming was larger in the south by 2010. In general, annual precipitation had increased by 10% across all latitudes in central Siberia, and only in the extreme south, in closed intermountain hollows did precipitation decrease by 10% or more. Growing season length has been increasing as well, accompanied by increasing vegetation productivity (Shulgina et al., 2011). Arctic ice and mountain glaciers have decreased, retreated, or even disappeared. Snow cover tends to show complicated patterns, with increases in snow depth and a decrease in the duration of the snow cover season in European Russia and in northern West Siberia, while there are decreases in snow depth and the duration of snow cover season in southern Siberia (Bulygina et al., 2009).

Significant temperature increases in Siberia in the 21st century are expected to have profound effects on vegetation directly (Tchebakova et al., 2003; Soja et al., 2007) and indirectly through increased permafrost thawing and forest fires (Tchebakova et al., 2009). According to Weber and Flannigan (1997), an altered fire regime may be more important than the direct effects of climate change in forcing or facilitating species distribution changes through migration, substitution and extinction. Thus, climate change may have greater effects on temperate and boreal forests than on other forest ecosystems (Pastor & Post, 1988; Shugart & Smith, 1996), and both ecosystem shifts and structural changes in vegetation composition are predicted across Siberia (Tchebakova & Parfenova, 2006, 2010; Tchebakova et al., 2009a, b; Soja et al., 2007). The boreal forest of Eastern Eurasia is expected to have increased cold season albebo in its northern zone under a warming (where larch would be replaced by dark conifers), and reduced cold season albedo in its southern zone (where dark conifers are expected to be replaced by deciduous trees in moist areas or by grasses in drier regions) (Zhang et al., 2009).

Belotelov et al. (1996) simulated the consequences of climate change for the vegetation of Russia. All their experiments demonstrate similar tendencies in biome boundary motion, but the results are quite different. According to their results, biomes are moving to the north and a new type of biome (scrubland) will appear in the European part of Russia, while grassland and cold dry scrub will spread significantly. In the simulations, the zone of forest grew and the grass and scrubland zone increased as well. The zone of tundra is predicted to increase during the first 40-50 years due to the fast expansion of the biome to the North, but then it will begin to decrease due to boreal forest expansion. The rate of changes depended on the rate of vegetation migration included in the experiments.

Zhang et al. (2009) report climate-change simulation results for 23 sites in Russia. In Vladivostok, *Fraxinus* (ash) becomes the dominant species replacing *Pinus* (pine) according to simulations. *Pinus* and *Abies* (fir) retain their biomass until the end of the transient change in climate and then a sudden dieback of coniferous trees takes place in

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years 1,150–1,160. After this transient response, there are no evergreen trees remaining in the forests of Vladivostok. In Poronaysk, the biomass of *Pinus* increases and the forests become *Pinus/Picea* co-dominated. In Huma, *Fraxinus* gains dominance in the forests and there is a pronounced decrease in coniferous taxa, notably *Abies*. In Mohe, Vitim, Olyekminsk and Tura, an increase in species richness is expected in the forests, due to warmer conditions and an increase in precipitation. As a consequence, the dominant genus, *Larix* (larch) would have more competition and decrease strongly. It would become absent in 100 years, and the forest type would transition from broadleaf/*Larix* forests to deciduous forests. It can be seen that the nature of change is site-specific and the change in composition does not strongly develop until 100 or 200 years after the climate change has been initiated. An exception to this general pattern can be observed in *Abies*, which can have profound decreases in a relatively short period of time with climate change.

In general, simulations indicate that the total biomass of the forests will not significantly increase and may even drop in the western area of the Eastern Eurasian region. Simulations do not represent tree line expansion in highlands and in the northern tundra zone under future climate change. However, the forest composition is predicted to change significantly. The southern boundary of the boreal forests may move northward and several boreal conifer species such as *Larix*, *Abies* and *Picea* (spruce) may either become locally extinct or retreat to higher elevations in the future. However, migration of these trees into northern Eurasia could be significantly delayed by lack of tree seed sources in the far North. *Pinus* will become the major regional tree genus in the southeastern sites of East Eurasia, replacing the currently dominant *Abies/Picea* forests. The distribution of *Larix* is predicted to shrink and move from East to West. In contrast, the biomass and distribution of deciduous broad-leaved trees such as *Fraxinus*, *Quercus* (oak) and *Tilia* (lime) is expected to increase significantly and expand to northwest and southeast. *Betula* (birch), which has tolerance to drought and high adaptability to temperature, will expand its distribution as well and dominate the forests in the north-western region instead of *Larix*. As a consequence, the East Eurasia region may become mainly dominated by broad-leaved deciduous forest, mixed forest and some evergreen needle leaved forest (*Pinus-Abies/Picea* forest). However, Zhang et al. (2009) also add that most simulated forests will be relatively unaffected by a small range of climate change and maintain the existing forest structure before producing a transient response.

Shuman et al. (2011) predict that warmer climate will likely convert Siberia's deciduous larch forests to evergreen conifer forests, particularly the low-diversity regions in central and southern Siberia can experience an abrupt vegetation shift.

The tundra-taiga boundary is probably the Earth's greatest vegetation transition, where a rapid and dramatic invasion of the tundra is expected by the taiga (Callaghan et al., 2002). Besides, this boundary is becoming increasingly affected by human activities that degrade forest-tundra into tundra-like areas. In the Polar Urals, Devi et al. (2008) observed that the forest has been expanding upwards into the formerly tree-free tundra during the last century by about 20-60 m in altitude, which disagrees the results of Zhang et al (2009). This forest expansion coincided with significant summer warming and a doubling of winter precipitation during the 20th century. The same is confirmed by Kirdyanov et al. (2012), who found a strong and successful germination of larch (*Larix sp.*) at the current upper tree line, indicating an ongoing densification of a formerly open forest and an upslope shift of the tree-line position.

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Svirezhev (2000) calculated the shift of the transition zone between taiga and steppe in central Siberia. In this region the annual temperature is expected to rise by 5 °C and the precipitation will increase by 10%. The border between taiga and forest-steppe zones will be shifted northwards by 1.018°~113 km, and the border between forest-steppe and steppe zones will be shifted northwards by 0.723°~80.25 km. As a result, the width of the transition zone between taiga and steppe will increase by 33 km under climate change.

Simulations by Tchebakova et al. (2009a) show that Siberian vegetation would be altered before 2020, and vegetation zones would be severely altered by 2080. According to the moderate scenario, habitats for northern vegetation classes (tundra, forest-tundra and taiga) would decrease significantly, enabling southern habitats (forest-steppe, steppe and semidesert) to expand. According to the harsh scenario, northern vegetation types would decrease to an even greater extent, and tundra and forest tundra would remain as only remnants, with temperate southern vegetation prevailing on 50% of Siberia. Biomes could shift northwards as far as 600-1000 km and tree lines have shifted northwards and upslope in both the plains and mountains (Tchebakova et al., 2011). Tchebakova et al. (2009a) assume that vegetation is capable of adjusting to the predicted changes, however, the redistribution of forest zones will require long periods. Migration of boreal tree species, as estimated from paleoecological evidence, may have an average rate of only 300-500 m/year (King & Herstrom, 1997), although maximal rates could approach 5 km per year (Kirilenko & Solomon, 1998). In the mountains, tundra may be replaced by forest more rapidly. The upper tree line is predicted to shift upwards in elevation by about 400 m, and the lower tree line is expected to shift upwards by about 250 m (Tchebakova & Parfenova, 2006, 2010; Tchebakova et al., 2009a, b; Soja et al., 2007). However, tree movement upslope may be tempered by poorly developed and thin soils in high mountains; consequently, it may take a millennium for the tundra zone to be completely replaced by forest. Besides, forest and tundra species extinction is also a possibility (Tchebakova et al., 2011). Since the future climate is predicted to be drier, forest-steppe and steppe, rather than forests, would be the dominant vegetation type over half of Siberia. Besides, desertification is expected in extreme southern Siberia as a result of decreasing precipitation while temperatures are increasing dramatically (Tchebakova et al., 2009a, 2011). New habitats (broadleaf forest and forest-steppe) may also appear by 2080.

Currently, permafrost covers 80% of Siberia and is the primary factor controlling the distribution and composition of forests, particularly in interior Siberia (Tchebakova et al., 2009a). Forest growth in high latitudes is not only limited by temperature, radiation and nutrient availability but also by the availability of liquid soil water (Beer et al., 2007). Thus, permafrost limits the northward and eastward progression of dark conifers (*Picea obovata, Pinus sibirica* and *Abies sibirica*) and light conifers (*Larix sibirica* and *Pinus sylvestris)*. However, due to climate change, an increased thawing of the active layer depth is expected, and the permafrost boundary is predicted to retreat to the north and east. As a result, dark conifers will expand their distributions northwards (Kharuk et al., 2005) as forests have progressed into the tundra during the last 40 years as well (Kharuk et al., 2004). However, since permafrost will not thaw deep enough across Siberia, the East Siberian landscape is expected to be populated with larch (*Larix dahurica*). In the moist climates of West Siberia and with permafrost melting, spruce (*Picea obovata*) and *Pinus sylvestris* (Scots pine) could outcompete larch (*Larix sibirica*) (Utkin, 2001; Polikarpov et al., 1998). In the transition zone between dark-

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needled and light-needled tree species, birch and mixed conifer-hardwoods would dominate (Polikarpov et al., 1998). As a whole, retreating permafrost should cause a reduction in the area of forests and their replacement by steppe on well-drained, tilted geomorphology (Lawrence & Slater, 2005) or by bogs on poorly drained, flat geomorphology (Velichko & Nechaev, 1992).

Wildfire is a catalyst for maintaining stability and diversity in boreal forests in synchronization with the climate (Tchebakova et al., 2009a). Fire danger is predicted to increase as climate is warming (Stocks et al., 1998). Furthermore, a drier climate would result in increased tree mortality in the southern taiga, thus increasing fire fuel accumulation. As a consequence, risks of large fires would significantly escalate in southern Siberia and in central Yakutia, promoting new habitats for steppe and forest-steppe rather than for forests (Rizzo & Wilken, 1992; Smith & Shugart, 1993; Tchebakova et al., 2009a).

Nevertheless, more hot spots of forest expansion were modeled at the expense of tundra and less hot spots of steppe expansion were modeled at the expense of forest by Tchebakova et al. (2011). Potential albedo feedbacks due to land cover change and a longer snow-free period may result in additional regional warming in the north, promoting further forest advancement into the tundra, and the southern cooling could promote the maintenance of the forest-steppe ecotone (Tchebakova & Parfenova, 2010).

Yu et al. (2011) investigated tundra plant communities on the Yamal Peninsula, in northwest Siberia. They found that compared to climate change, grazing had a more substantial effect on plant communities. According to simulations, grazing caused total plant community biomass to decrease, most plant functional types were negatively affected, particularly lichen and deciduous shrubs. However, evergreen shrub biomass increased as grazing intensity increased. Nevertheless, this may not represent the situation that can be seen in the field on the Yamal Peninsula (Walker et al., 2010), one reason may be that the susceptibility of vegetation to reindeer trampling has not been taken into account in the model. According to van der Wal (2006), increased grazing may favour moss growth as well, possibly causing the tundra plant community to shift from lichen-dominated tundra to moss-dominated. Besides, when evergreen shrub growth rate was reduced, the proportional abundance of moss and graminoids increased with continual increase in grazing pressure, resulting in the plant community transition from shrub-dominated tundra toward moss- and graminoid-dominated tundra (Zimov et al., 1995; Forbes et al., 2009; Yu et al., 2011). Simulations show that evergreen and deciduous shrubs responded to both transient and equilibrium warming scenarios with continued positive responses. Graminoids and forbs responded to transient warming with greater biomass increase than to equilibrium warming, which may be due to shifts in controlling mechanisms from direct warming response to species competition for nutrients (Epstein et al., 2000). Lichens responded to transient warming with only a little biomass increase and had a biomass decrease during equilibrium warming when grazing was present. Shrub expansion and greening trends in the Arctic, presumably caused by warming, have been observed by several other authors as well (Sturm et al., 2001; Tape et al., 2006; Jia et al., 2003; Goetz et al., 2005; Bhatt et al., 2010), while Forbes et al. (2010) found a significant increase in shrub willow (*Salix sp.*) growth over the last six decades. It was confirmed in other studies as well that moss and lichen biomass declined in response to warming in Low Arctic sites, while deciduous shrubs and graminoids increased (Chapin et al., 1995; Henry & Molau, 1997; Walker et al., 2006). Yu et al. (2011) conclude that warming interacts with grazing and may

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contribute to complicated plant responses. In general, grazing negated plant biomass increases in response to warming. Deciduous shrubs responded to warming with increased biomass, and the increases were profound at lower intensity grazing regimes.

Summary list of the main ideas and phenomena

- direct causes of changes in vegetation: elevation of CO_2 concentration, increase in temperature, changing precipitation patterns
- indirect causes: changing biotic interactions, fire regime, nutrient availability, water availability, land use, grazing, nitrogen deposition, invasive species and permafrost thawing
- different types of changes: phenological, physiological, distributional
- changes on different levels: species, community and ecosystem level
- how do distributional changes take place on the different levels?
  species / populations: colonization and extinction
  communities: changes in structure and composition
  biomes: shifts, motion of boundaries
- migration is expected
  will species be able to keep pace with climate change?
  rate of migration depends on the rate of climatic changes and on limiting factors
- limiting factors (abiotic and biotic constraints): fragmentation of the landscape, land use, grazing, seed availability, resource availability, dispersal capabilities of individual species, available space, geographical barriers, topography, soil types, biotic interactions
  in most models, only some of the limiting factors are considered
  migration is mostly considered either as no migration or as unlimited migration
- uncertainties
- lags are likely between climate changes and biotic responses, especially in lowland areas → possible extinctions
- individual species respond differently (from extinction to large increases in ranges) and geographical variability in responses
- literature: field studies, experiments, modelling studies / simulations, reviews

Global changes:

- vegetation models differ regarding types, global circulation models, emissions scenarios, time slices, migration and land use and other factors considered or not, vegetation/biome classification, emergence of new communities considered or not → uncertainties
- some authors presume the collapse of the North Atlantic thermohaline circulation but most of them do not → cooling or warming of the northern hemisphere is predicted
- not clear whether increasing or decreasing net primary production, large drought-induced declines or large vegetation expansions in early stages can be expected
- latitudinal and altitudinal shifts (polewards and upwards)
- advance of tree line and forest diebacks

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- the greatest change in boreal and temperate zones
- temperate mixed forest, boreal conifer forest, tundra and alpine biomes show the highest vulnerability
- shift of taiga into the present areas of tundra
- reduction of cold deciduous forest, tundra, subtropical forests and nival area and increase of cool mixed forest, tropical thorn woodland and cool temperate moist forest; increase of cool conifer forest and taiga is controversial
- change in tropical forests is uncertain
- all polar/nival, subpolar/alpine and cold ecosystem types would have a continuously decreasing trend, while all tropical ecosystem types would increase, except tropical rain forest
- the Mediterranean biome is threatened by desertification
- new, non-analogue biomes/communities, ecological surprises may emerge

The Alps and Switzerland:

- mountain regions tend to warm more rapidly → they are particularly vulnerable
- upward shift of species, increase in species richness on mountain tops and increase of the floristic similarity of the summits – due to climate warming or a natural dispersal process?
- significant reduction of the alpine vegetation belt, strong reductions in the area available for alpine species → local extinctions ("summit traps")
- upward shift of the forest limit, tree line and tundra line
- montane forests dominated by deciduous trees move toward a higher elevation, subalpine coniferous forests shift into the alpine belt, colonisation of the nival belt
- montane beech-fir communities shift to beech communities, beech-dominated forests replaced by oak-hornbeam forests in the northern Alps
- invasion by naturalized exotic laurophyllous species in the southern Alps
- increasing drought risk → collapse of forests in some areas
- subalpine grasslands are relatively stable

Scandinavia:

- upward movement of altitudinal range-margins of plant species and bioclimatic zones and rise of the tree limit
- extension of the boreal forest northward and to higher elevations
- a shift in dominance from Scots pine to deciduous broadleaved trees in some regions
- emergence of non-native tree species
- alpine grasslands are replacing snow bed plant communities
- *Dryas* replaced by graminoids and forbs → meadow from the heath

Western Europe:

- forest transformation from Norway spruce to European beech
- decreasing abundance of beech
- grasslands replacing heathlands or heather displaced by bracken

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- unproductive, grazed grasslands are stable

Southern Europe:

- water availability is the most important environmental constraint → extremely vulnerable to climate change
- fire plays a significant role
- overall decrease of forest cover
- potential extinction among endemic species
- decreasing abundance of mesophilous plant species and increasing abundance of xero-thermophilous ones
- dieback of some dominant tree species like Scots pine, decline of *Pinus nigra*, reducing distribution area of *Fagus sylvatica*
- shift from pine dominated to broadleaf (oak) dominated forests
- beech forests and heathlands replaced by holm oak
- upward shift of species and decreasing alpine vegetation
- high-mountain grassland communities replaced by shrub patches
- subalpine grasslands are especially vulnerable, shifts in dominance from grasses to forbs
- invasion is likely

Central Europe:

- shift of vegetation belts upwards
- coniferous forests converted to deciduous forests, reduction of mesic beech forests and Dinaric fir-beech forests, increase in thermophilous forests
- upward shift of the tree line

Russia:

- main drivers of vegetation changes: climate change, increased permafrost thawing and forest fires
- biomes are moving to the north
- upward shift of the tree line
- zone of tundra is predicted to increase first and decrease afterwards, invasion of the tundra by the taiga
- in tundra plant communities, grazing has a substantial effect as well and may cause shifts in dominance
- shrub expansion and greening trends in the Arctic
- total biomass of the forests will not significantly increase and may even drop, significant changes in forest composition
- in Eastern Eurasia: larch replaced by dark conifers, in Southern Siberia: dark conifers replaced by deciduous trees in moist areas or by grasses in drier regions
- conifer species becoming locally extinct or retreating northwards and to higher elevations
- shrinking distribution of *Larix*
- increasing distribution of deciduous broad-leaved trees

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- in the transition zone between dark-needled and light-needled tree species, birch and mixed conifer-hardwoods
- forest-steppe and steppe, rather than forests, would be the dominant vegetation type over half of Siberia, desertification is expected as well

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